THE STRUCTURE OF SIMBLUM SPHAEROCEPHALUM

HENRY S. CONARD

(WITH PLATES 96 AND 97)

In October, 1911, Miss Winnie Gilbert, a student at Grinnell College, Iowa, brought in a specimen of the pink stink-horn, *Simblum sphaerocephalum* Schlecht. It was found on the north side of a deep railroad cut one mile west of Grinnell. Further search in this place resulted in the collection of several mature specimens and a number of "eggs." They grew about half way up the slope, facing south, on Marshall silt loam that had slid down the bank many years ago, and at about the level of the boundary between the loess and the glacial drift. Perhaps there are special moisture conditions at this level, though other vegetation does not suggest this. With them was *Poa pratensis* as dominant plant, as well as seedlings of *Acer negundo, Physalis* spp., *Aster* spp., etc. Two or three weeks later my colleague, Professor H. W. Norris, found specimens on a hillside above Skunk River, three miles southwest of Turner Station (southeast corner of section 5, Richland Township, Jasper County, Iowa). Some of the smaller "eggs" were cut open and killed in chromacetic fluid and later sectioned on the serial microtome. The rest of the material was preserved in alcohol. The following studies were made of the preserved material. My best alcoholic specimens have since been deposited with Professor Macbride at the State University of Iowa, Iowa City. A brief account of this find was presented to the Iowa Academy of Science in April, 1912.[1]

Simblum sphaerocephalum was originally described by Schlechtendal (1861) from Argentina, where it is common. Similar plants have been collected in southern Brazil and in Venezuela, and described under different names. In North America it is known from Astoria and Cold Spring Harbor, Long Island;

[1] Proc. Iowa Acad. Sci., 19: 103. 1912.

Nebraska; Kansas; Washington, D. C.; Talbot County, Md.; and Texas (Lloyd, 1909, p. 67; Long, 1907). We follow Fischer (1890, p. 59) in reducing to synonymy the names *S. rubescens, S. australe, S. Lorentzii,* and *S. pilidiatum.* In view of the rarity of this plant in the United States, we offer the following detailed observations.

The white volva, flesh-pink stalk and receptaculum, and umber-brown spore-mass make this fungus a curious and striking object (fig. 5). Its odor is somewhat nauseous, but not strong. The size of our plants is shown by the following tables of measurements:

MEASUREMENT OF MATURE PLANTS, IN CM.

Total Height	Length of Stalk	Length of Head	Diameter of		
			Head	Stalk	Volva
5[2]	3	1	1.75	1.2	2.3
7	6.3	0.7	1.8	1.3	
5.5		0.7	1.3	1.0	
8.5	6.5	1.5	2.5	2.1	3
10 (?)	8.0	1.5	2 (?)	1.8	3
7	5.8 (?)	1.0	1.5	1.3	
5.5	4.3 (?)			1 (?)	
					2.5[3]

MEASUREMENTS OF "EGGS," IN CM.

Height.	Diameter.	Rhizomorph.
2.2	1.5	
2.6	1.7	1.9
2.9		
2.3	2.15	3.0
1.9	1.6	
	1.5	

When lifted carefully each plant was found to have a stout white rhizomorph running into the ground (figs. 1, 5). These strands are smooth, solid, and gently tapering. The longest we have is 3 cm. with a diameter of 2 mm. The egg-stage is obconical in shape (fig. 1), white, rather firm to the touch, but not turgid. When cut in half lengthwise the "egg" shows first a tough, white peridium (fig. 1), then a thick layer of firm, translucent, gelatinous matter traversed by strands or trabeculae of denser white tissue. On comparing cross-sections (fig. 2) it is seen that these

[2] Including rhizomorph.

[3] Has also a rhizomorph 2 cm. long.

strands are really anastomosing partitions, connecting with the peridium externally and with the bars of the receptaculum within. The gelatinous layer is therefore divided up into many irregular longitudinal chambers. A similar arrangement of partitions in the volva jelly is described by Fischer (1901) in *Simblum periphragmoides,* and by Long (1907) in this species.

So far as is shown by the rather advanced stages at our disposal, *Simblum sphaerocephalum* agrees precisely in structure with other Clathraceae as described by Fischer (1890–1910). The stalk of the receptaculum is traversed by a central strand, (*S*) of gelatinous hyphae, which is continuous with the gelatinous filling of the chambers of the stalk (figs. 1, 3). The pseudoparenchymatous tissue is composed of small spherical cells, arranged in a network of anastomosing plates which form the walls of the chambers (figs. 3, 7, 8). These walls are much folded in the egg stages. Though the chambers seem to be all connected with one another and with the central cavity of the stalk, they do not connect definitely with the tissues surrounding the stalk. Elongation of the stalk is manifestly due to a great increase in size of the pseudoparenchyma cells, as shown by figures 7 and 8. Though these are not taken from the same plant, their evidence seems conclusive. Coupled with this enlargement is a general expansion of the stalk in all directions, a straightening of the folds of the chamber walls, and liquefying of everything except the pseudoparenchyma.

In the head region, the bars of the receptaculum (*Rp*) are found on the surface of the gleba, in full view when the volva-jelly is removed. From each bar a plate of permanent hyphal tissue (*Pl*) extends to the peridium. Since the receptaculum is net-like, these plates enclose prismatic spaces (*G*) which correspond in position and number to the meshes of the network. It is in these spaces that the volva-jelly is contained. In our specimens (and also in *S. periphragmoides,* according to Fischer, 1901) these spaces bend downward parallel to the stalk, and end near the base of the "egg." Doubtless they originate when the "egg" is very young, and before the stalk is formed (Cf. text fig. 1, *G*). As growth proceeds, the volva extends by enlargement of its upper parts (above ϕ, text fig. 1), and the stalk is

intercalated beneath the head. Meanwhile the plates elongate *pari passu,* resulting in the condition shown in text fig. 3. If this be true, as seems almost certain, the stalk would seem to be an organ of much more recent origin than the head of the receptaculum. It may be regarded as an extreme development of the basal ring of the receptaculum of *Clathrus* (text figs. 1, 2, α). This agrees with the generally accepted view that *Clathrus* is one of the most primitive of the Clathraceae.

Fischer (1890, p. 11) supposes that the difference between the early stages of development of *Simblum* and *Clathrus* would be that in the former the branches of the central strand come off

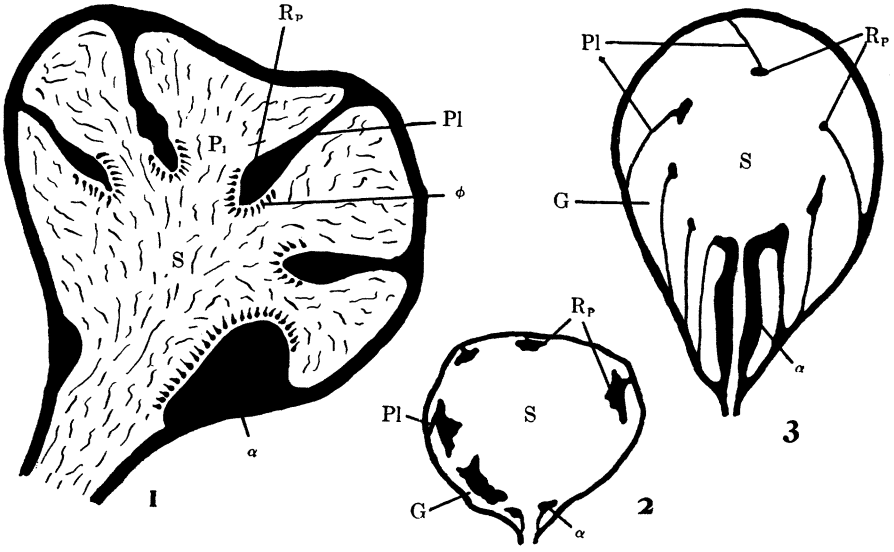


FIG. I.—1. Vertical section of very young egg of *Clathrus cancellatus,* from Fischer 1890, pl. 1, f. 3.—2. The same, mature egg; l. c. f. 6.—3. Diagram of vertical section of mature egg of *Simblum sphaerocephalum, a* lowest ring of receptaculum; other letters as in plate.

higher up than in the latter ("Der Unterschied der ersten Fruchtkörperanlage von *Simblum* gegenüber derjenigen von *Clathrus* besteht also darin, dass vom Centralstrang hier erst weiter oben als dort Zweige abgehen"). But if the central strand branches higher up, there should be no volva-jelly around the stalk—unless the branches force themselves down between the layers of the peridium and the plates, parallel to the stalk. It seems much

more reasonable to say that the branching of the central strand takes place when as yet there is no stalk, exactly as in *Clathrus* (text fig. 1). The branches are then fixed to the peridium, as it were, at their outer ends. When their inner ends are raised up by the intercalation of a stalk, the outer parts of the branches are drawn out into vertical columns, parallel with the stalk. Thus the stalk of *Simblum,* originating as a sterilized basal portion of the receptaculum, becomes an independent organ, bearing the fertile receptaculum at its upper end. The usefulness of such a stalk for the better distribution of the spores, as Moeller (1895) suggests, cannot be doubted.

From a study of Burt's (1894) description of *Anthurus borealis* and Fischer's (1910) of *Aseroe,* it appears that in these forms also the stalk develops in the manner outlined above, rather than by a branching of the rudiment of the central strand higher up, and a forcing of the tips of the branches downward between the layers of the peridium. Indeed this view was mentioned as probable by Burt (1894, p. 495). It is indicated also by Moeller's description of the development of *Colus Garciae* (1895, p. 39). A study of the plates in the volva-jelly of *Colus hirudinosus, Kalchbrennera,* and *Laternea* would be helpful in this connection. Tulasne's (1846) figure of the egg of *Colus hirudinosus* shows the plates from the fertile parts of the receptaculum to the volva, but shows no plates in the region of the stalk. His figure 16 is a transverse section of the fertile portion and figure 15 an outside view of the entire egg. The matter is therefore not settled for this species.

In *Lysurus, Anthurus* and *Aseroe* it is possible to consider the stalk as a fusion of the lower vertical bars of a clathrate receptaculum. *Clathrella chrysomycelina* and *Laternea* apparently lead to such a view. In *Simblum* there is no indication whatever of such an origin. Now, in all stalked Clathraceae, the stalk is surrounded by a sheath of gelatinizing hyphae, to which the plates attach, as in *Simblum.* But in the fertile portion the plates attach directly to a line or furrow along the arms or branches of the receptaculum. It seems reasonable therefore to believe that the stalks are homologous structures throughout the family, and of the same nature as described for *Simblum.* The sheath of the

stalk is then the place of attachment of the plate tissue to the lowest horizontal bars of the receptaculum, which has become extended into a sheath as the bars elongated to form the stalk.

The superficial position of the bars of the receptaculum in the head of *Simblum sphaerocephalum* has already been remarked (fig. 1). In this it differs markedly from *S. periphragmoides* (Fischer, 1893, 1900, 1901) whose bars are deeply embedded in the gleba. On critically examining the relation of gleba to receptaculum, we find in many cases gleba-chambers bounded on one side by fertile hymenium and on the other by pseudoparenchyma of the receptaculum-arm (figs. 9, 12). The transition from hymenium to pseudoparenchyma, however, is not gradual, but abrupt. Sometimes a narrow strip of tramal tissue lies between them. In many cases it is evident, so far as sections can prove, that the tramal hyphae are continuous with the pseudoparenchyma (fig. 10). Thus the pseudoparenchyma has a double origin. Indeed one frequently finds cavities separating the portions of different origins (fig. 10). These facts support Fischer's view, proposed in 1890, and proven for *Dictyophora irpicina* in 1910 (*b*), that the pseudoparenchyma represents sterile hymenial tissue, or a hymenium of paraphyses without basidia. In this case the cavities in the pseudoparenchyma of *Simblum* may be considered to be rudimentary gleba-chambers (fig. 10, *f*). Burt (1894) maintained that the pseudoparenchyma of *Anthurus borealis* is of strictly "cortical" nature, and has no connection with the surrounding gelatinizing hyphae. This idea was apparently drawn chiefly from sections in the stalk region, where the tissues are much more sharply separated. After the first rudiments of the stalk are formed as the lowest mesh of a net-like receptaculum, according to our theory, the further development of the stalk tissues may be quite independent of one another. Thus Burt's observations would be entirely right, and in no contradiction with Fischer's (1900) and my own. In one of my plants of *Simblum* two bars of receptaculum tissue were found near the center of the head, completely embedded in the gleba (fig. 6). Following these upward, they joined one of the upper bars of the receptaculum. Another specimen showed bars of the receptaculum extending deep into the gleba. These irregularities might

easily occur if hymenium and pseudoparenchyma are homologous tissues. Certain patches in the midst of the branches of the central strand in some of my sections give an appearance, in texture and staining, of a tissue intermediate between hymenium and pseudoparenchyma. Unfortunately gelatinization is so far advanced that no details are available. The center of each patch is occupied by numerous globular bodies of about the size and color of spores.

Fischer's (1890, p. 7) suggestion that the hymenium is fertile wherever it lines a cavity and sterile when two layers are appressed without a space between, is untenable. Not only is pseudoparenchyma developed adjacent to gleba-chambers (fig. 9), but basidia are borne in such narrow chambers that the space is literally obliterated (fig. 12). Moeller (1895, p. 31) has already emphasized these objections to Fischer's view. The stimuli which guide the development of an embryonic tissue must be much more profound than this.

The gleba of *Simblum sphaerocephalum* is traversed by stouter strands of tissue similar to that of the trama, constituting the "branches of the central strand (*P*)" of Fischer. Each such branch (figs. 1, 11) runs radially outward from the central gelatinous tissue of stalk and head, to merge into the volva-jelly at the middle of one of the meshes of the receptaculum. Each mesh is traversed by one such branch. Some branches are rod-like and reach the surface of the gleba in a circumscribed spot. Others are ribbon-like, and form a line on the surface of the gleba. Tangential sections of the surface of the gleba show the gleba-chambers as narrow branching slits radiating from the branch of the central strand and nearly at right angles to the bars of the receptaculum. This indicates an origin such as Fischer has described in other Clathraceae. The chambers probably result from the growth of trama-plates from the branch of the central strand toward the bars of the receptaculum. But no order was found elsewhere in the arrangement of the trama-plates or gleba-chambers.

In all of our material the dense mass of spores hides the basidia. Probably these had already begun to gelatinize. We found one basidium, apparently in normal condition. It was

nearly globular (fig. 4), with a short constricted base, and two short sterigmata at the apex. The basidium is about 2.5 μ in diameter and 4.5 μ tall, with sterigmata about 0.5 μ tall. The spores are ellipsoidal, with a single large nucleus, and measure 3 μ by 1.5 μ. These dimensions, so characteristic of Phalloids, are of the same order of magnitude as those of bacteria—a fact which coincides with the idea that both of these groups of plants are distributed by flies.

SUMMARY

1. *Simblum sphaerocephalum* Schlecht., a common fungus in parts of South America, is now known from New York, Maryland, District of Columbia, Iowa, Nebraska, Kansas, and Texas. It shows every essential character of the Clathraceae.

2. The stalk elongates by enlargement of the cells of the pseudoparenchyma.

3. The bars of the fertile receptaculum are superficial on the gleba.

4. The plates which divide the volva-jelly are vertical in the region of the stalk, enclosing a mass of jelly for every mesh of the receptaculum. Their position is believed to be due to the late development of the stalk in a rudiment which would be identical in early structure with that of a *Clathrus*. The stalk of *Simblum* is therefore a highly developed basal ring of a clathrate receptaculum, and not a fusion of vertical columns.

5. Pseudoparenchyma of the receptaculum may be regarded as sterile hymenium.

6. In the superficial portions of the gleba, at least, the chambers originate by growth of trama-plates from the branches of the central strand toward the receptaculum-arms.

For use of the literature which has made this paper possible, I am indebted to the generous loan-system of the Missouri Botanical Garden. To the officers of the Garden I wish to extend hearty thanks. The photomicrographs are by Mr. Paul M. Smith.

BIBLIOGRAPHY

1. **Burt, Edw. A.** A North American *Anthurus*—its Structure and Development. Memoirs of the Boston Society of Natural History 3: 487 ff. 1894.
2. **Fischer, Ed.** Untersuchungen zur vergleichenden Entwicklungsgeschichte und Systematik der Phalloideen. Denkschrift der Schweizerischen naturforschenden Gesellschaft **32**: 13 ff. 1890.
3. **Fischer, Ed.** Neue Untersuchungen, etc., l. c. **33**: 10 ff. 1893.
4. **Fischer, Ed.** Untersuchungen, etc., III Serie, l. c. **36**: 71 ff. 1900.
5. **Fischer, Ed.** Einige Bemerkungen über der von Herrn Prof. Schröter aus Java mitgebrachten Phalloideen. Vierteljahrschrift der naturforschenden Gesellschaft in Zürich **46**: 122–127. 1901.
6. **Fischer, Ed.** Die Fruchtkörper-Entwicklung von Aseroe. Annales du Jardin Botanique de Buitenzorg, II Sér., supplem. 3, p. 595–614. 1910 (*a*).
7. **Fischer, Ed.** Beiträge zur Morphologie und Systematik der Phalloideen. Annales Mycologici **8**: 316–321. 1910 (*b*).
8. **Lloyd, C. G.** Synopsis of the known Phalloids. Bulletin of the Lloyd Library No. 13, Mycological Series No. 4, Sept., 1909.
9. **Long, W. H.** The Phalloideae of Texas. Journal of Mycology **13**: 102–114. 1907.
10. **Moeller, Alf.** Brasilische Pilzblumen. Botanische Mittheilungen aus den Tropen, herausgegeben von A. F. W. Schimper, Heft 7. 1895.
11. **Schlechtendal, D. F. L. von.** Eine neue Phalloidee, nebst Bemerkungen ueber die ganze Familie derselben. Linnaea **31**: 101–194. 1861–62.
12. **Spegazzini, C.** Fungi Argentini novi vel critici. Annales del Museo nacional de Buenos Aires **6**: 184. 1899.
13. **Tulasne,** in Bory de St. Vincent, Cosson et Durieu de Maisonneuve, Exploration scientifique de l'Algérie. Sciences naturelles, Botanique, Acotyledones. Paris, 1846–49; pp. 435–439, *pl. 23*.

EXPLANATION OF PLATES

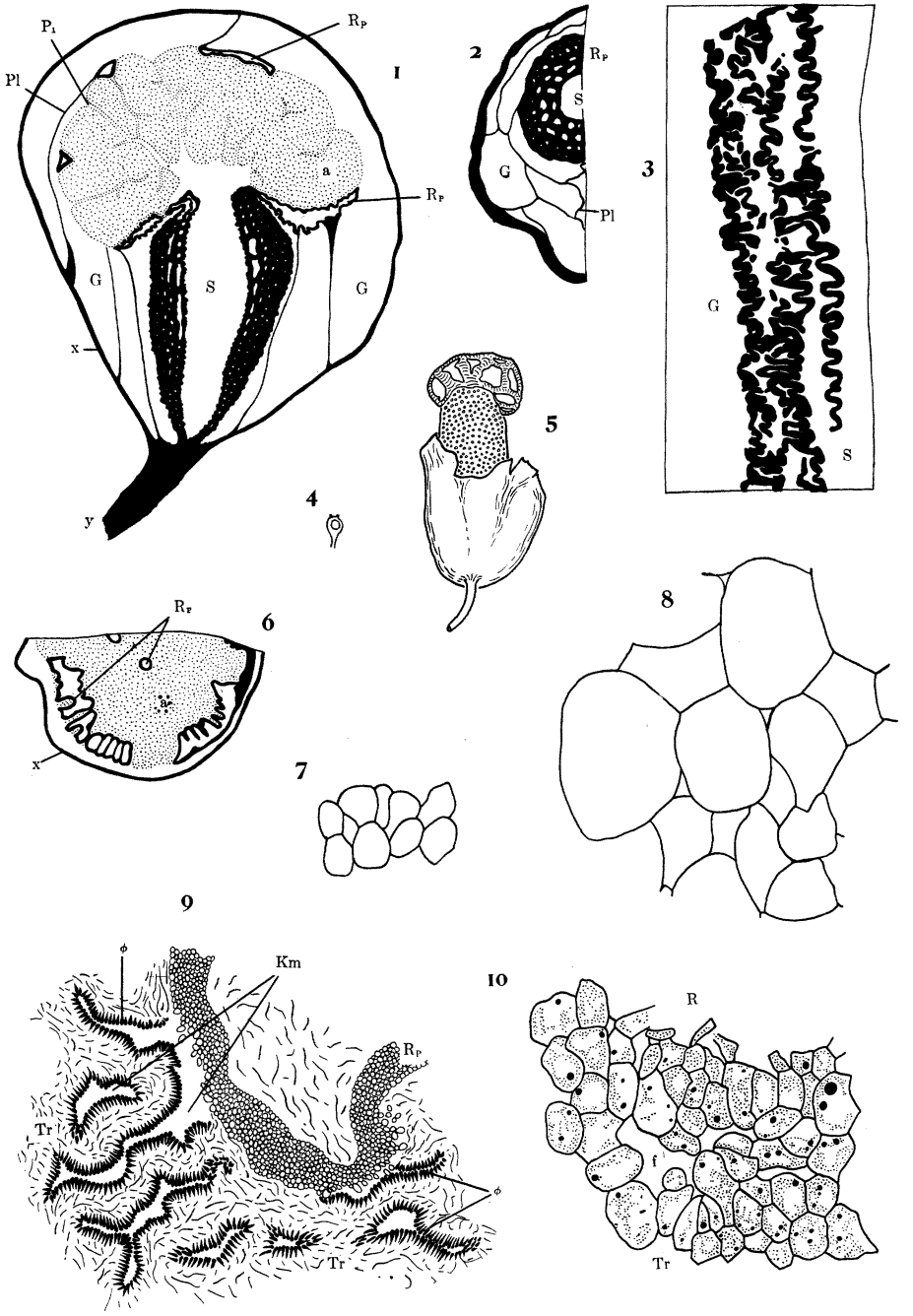
Key to index letters, the signs being mostly those used by Fischer. The figures are all of *Simblum sphaerocephalum*.

a, gleba.

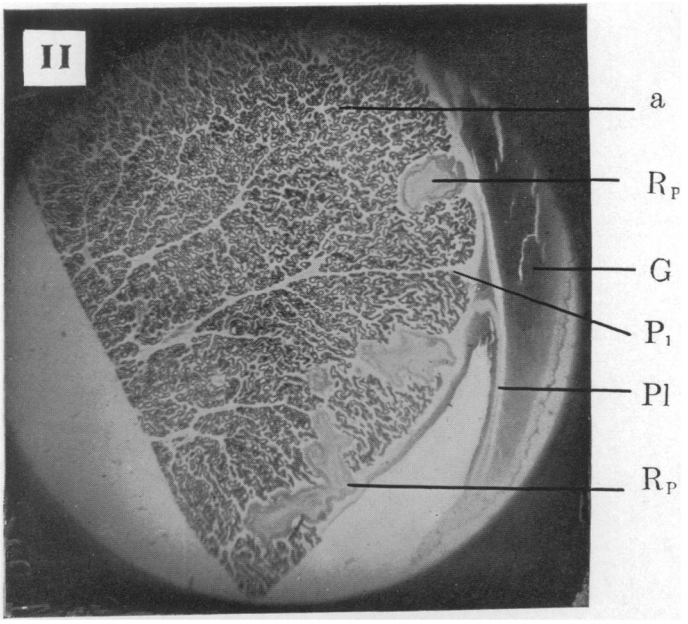
f, rudimentary gleba-chambers in pseudoparenchyma of receptaculum.

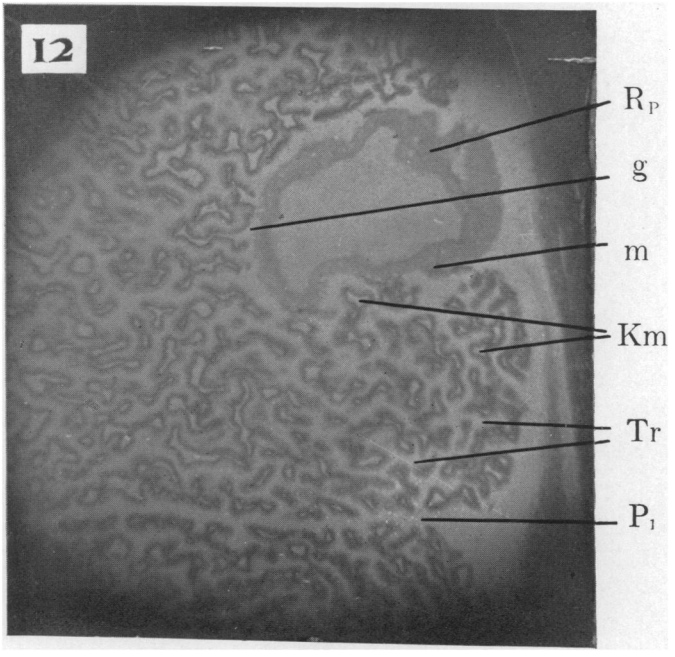
G, gelatinous part of volva.

g, gleba-chamber bounded partly by basidial layer and partly by pseudoparenchyma of receptaculum.



SIMBLUM SPHAEROCEPHALUM SCHLECT.





SIMBLUM SPHAEROCEPHALUM SCHLECT.

Km, gleba-chamber.
Pl, plate-like partition in volva-jelly.
P_1, branches of central strand.
R, cavity of arm of receptaculum (gelatinous).
Rp, receptaculum.
S, central strand of gelatinizing hyphae.
Tr, trama-plates.
x, peridium.
y, rhizomorph.
a, lowest ring of receptaculum.
φ, basidial layer (hymenium).

PLATE XCVI

1. Longitudinal section of nearly mature egg, measuring 2.35 cm. × 2.15 cm. Camera sketch.

2. Transverse section of egg through stalk, showing the partitions in the volva-jelly. Camera sketch.

3. Folded pseudoparenchyma tissues in longitudinal section of stalk in egg stage. The cavity of the stalk is on the right, *S*, and the volva-jelly (*G*) on the left. Camera sketch.

4. Basidium, from a microtome section. Camera drawing.

5. Mature *Simblum* 5 cm. tall. Camera sketch of alcoholic specimen.

6. Transverse section of halved egg, through middle of head. Camera sketch.

7. Cells of pseudoparenchyma of stalk from egg stage; camera drawing.

8. Cells of pseudoparenchyma of stalk teased out from a fully elongated specimen; camera drawing with same magnification as fig. 7.

9. Section of receptaculum arm and gleba; semi-diagrammatic camera sketch. From (*g*) in fig. 12.

10. Transverse section of pseudoparenchyma of arm of receptaculum, showing rudimentary gleba-chamber (*f*). Tramal tissue below (*Tr*) and cavity of arm (*R*) above. Camera drawing.

PLATE XCVII. PHOTOMICROGRAPHS

11. Transverse section of head of egg stage.

12. Portion of the same section, more highly magnified.

GRINNELL COLLEGE,
GRINNELL, IOWA.